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Diet of mid-Atlantic Sowerby's beaked whales *Mesoplondon bidens*

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ABSTRACT

The first mid-Atlantic diet of Mesoplodon beaked whales is presented, from ten Sowerby's *Mesoplodon bidens* stranded in the Azores region between 2002 and 2009. This doubles the worldwide number of stomachs sampled, and reveals new feeding habits for this species. The mean number of prey items per stomach was 85 ± 89 (range: 12–238), with fish accounting for 99.3% and cephalopods contributing less than 1% of total prey. Fish otoliths from 15 families and cephalopod lower mandibles from three families were identified, representing 22 taxa. The diet consisted mainly of small mid-water fish, the most numerous being *Diaphus* sp., *Lampanyctus* sp. and Melamphaidae species. Myctophids were present in all stranded individuals, followed by Diretmidae, Melamphaidae and *Opisthoproctus soleatus*, while the remaining fish species were scarce or single occurrences. Consistency of diet in four different years reveals a divergence from all previous records in continental areas, where mainly neritic and shelf-break benthopelagic fish species have been reported. Mid-Atlantic Sowerby's beaked whales' showed dietary plasticity, feeding on the most abundant mid-water groups occurring between 0 and750 m. Trophic level from prey numerical frequency was estimated at 4.4 ± 0.46.

1. Introduction

The unveiling of beaked whales' trophic role is still in its early days, mostly due to the scarcity of available data leading to few studies published on the diet of this group. Knowledge grows at the pace of stranding events and the lack of published material is particularly evident for *Mesoplodon* species, for which very low numbers of prey individuals are often found per stomach (e.g. Mead et al., 1982). Fish and cephalopods are the main diet components of the 14 species of *Mesoplodon* (MacLeod et al., 2003), with some species relying primarily on cephalopods (e.g. *M. carlhubsi* and *M. layardii*) and others on bony fishes (e.g. *M. mirus* and *M. bidens*).

The Sowerby's beaked whale *Mesoplodon bidens* (Sowerby, 1804) is exclusive to the North Atlantic and is the northernmost *Mesoplodon* in this ocean. Distribution extends from Massachusetts (USA) to Labrador (Canada) in the west, from Iceland and Norway in the north, along the European coasts down to Madeira Islands and along the Mid-Atlantic ridge to the Azores (Macleod, 2000). The species appears to be common in some parts of its range, with higher stranding reports from the British coasts and neighboring countries (Klinowska, 1991), but there is no information on its global or regional abundance. Present knowledge on the feeding habits of Sowerby's beaked whales is limited to thirteen stomachs from stranded and by-catch individuals from North America and European coasts, revealing a primarily piscivorous whale with preference for benthopelagic species (Dix et al., 1986, Santos et al., 1994, 1995; Gannon et al., 1998; Spitz et al., 2011).

The Azores archipelago and its surrounding seamounts rise east of the Mid-Atlantic Ridge, approximately at 36–39°N and 25–29°W, representing a residence or passage point for more than 25 cetacean species (Prieto and Silva, 2010). The steep topography of the region provides deep-water and slope habitats where most *Mesoplodon* species are commonly observed in continental areas, over the slope and beyond (e.g. Waring et al., 2001; MacLeod et al., 2004). *Mesoplodon* beaked whales frequent the mid-Atlantic ridge (Mar-Eco, 2004; Doksæter et al., 2008) and are common during summer in the Azores (Reiner, 1986; Leal, 2003; ICES, 2010 unpublished data), but little is known about their distribution and habitat preferences as elsewhere. There are scattered reports of Sowerby's beaked whales over slopes (Waring et al., 2001), canyons (Hooker and Baird, 1999) and deep oceanic waters (MacLeod et al., 2007).

This study provides the first insight on Sowerby's beaked whales' diet in the mid-Atlantic, based on ten specimens stranded

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in the month of July of 2002, 2004, 2005 and 2009. Dietary samples are compared between different years and with available information from other areas of its distribution. Prey choice and foraging strategy of Sowerby's beaked whales in the Azores is interpreted in light of the main preys' local abundance and habitat and current knowledge on the species.

2. Materials and methods

2.1. Sample collection

Researchers involved in the Azorean Stranding Network (RACA) carried out the necropsies and collected whole stomachs from ten Sowerby's beaked whales stranded between 2002 and 2009 (Table 1). All strandings occurred in the month of July in the central group of islands, four of which, of two and three individuals considered here as mass strandings (2002, 2005, 2009 Terceira and 2009 Faial; Table 1, Fig. 1). Stomachs were frozen and contents were subsequently sorted in the laboratory and preserved for later identification.

2.2. Prey identification

Full stomach samples were examined and sorted under a binocular microscope: otoliths were dry kept; all the other remains were stored in 70% ethanol. Fish otoliths and cephalopod lower beaks were identified using available keys for fish (Schmidt, 1968; Hecht and Hecht, 1981; Nolf, 1985; Smale et al., 1995;

Table 1
General information on stranded beaked whales in the Azores islands, between 2002 and 2009, with collection of stomach contents reported in this study; [f] indicates individuals found floating and towed to shore.

Code	Sex	Total length (cm)	Maturity[a]	Stranding			Stomach contents	
				Date	Location	Condition[b]	Fish otoliths	Cephalopod beaks
Mbi 02I	Female	432	M	27 July 2002	Pico[f]	3	Yes	No
Mbi 02II	Male	> 340[c]	–	29 July 2002	Pico	4	Yes	Yes
Mbi 04I	Female	413	M	19 July 2004	Pico	1	Yes	Yes
Mbi 05IA	Male	409	M	21 July 2005	Terceira	3	Yes	No
Mbi 05IB	Male	435	M	22 July 2005	Terceira	3	Yes	No
Mbi 09IA	Female	388	I	28 July 2009	Terceira	1	Yes	No
Mbi 09IB	Male	361	I	29 July 2009	Terceira	1	Yes	No
Mbi 09IIA	Female	410	M	30 July 2009	Faial	1	Yes	Yes
Mbi 09IIB	Female	414	M	30 July 2009	Faial	1	Yes	Yes
Mbi 09IIC	Female	384	I	31 July 2009	Faial	1	Yes	No

[a] Maturity established through external observation of the gonads: M—Mature; I—Immature.
[b] Condition: 1—Alive; 2—Freshly dead; 3—Moderately decomposed; 4—Decomposed.
[c] Minimum length. Total length could not be measured because the individual had a fractured beak.

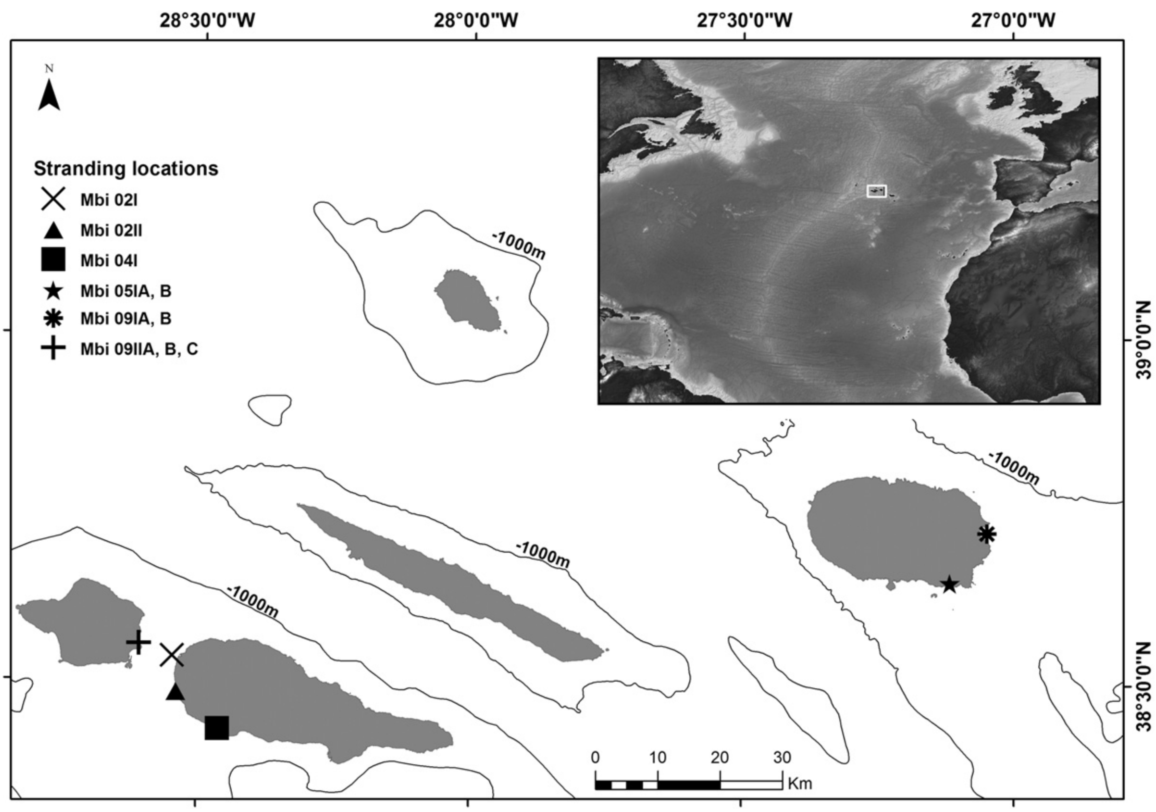

Fig. 1. Map of the Azores archipelago, with indication of stranding locations.

Tuset et al., 2008) and for squid beaks (Clarke, 1986), and reference collections of otoliths at the University of the Azores and Malcolm Clarke's personal cephalopod beak collection. Minimum number of individual prey was estimated from remains, as total upper/lower cephalopod beaks and right/left fish otoliths.

2.3. Data analysis

The importance of individual prey species is shown through their frequency in number (individual numbers of each prey). Frequency of occurrence was calculated for most frequent items only (percentage of samples containing each prey type). Diet overlap was assessed using Schoener (1968) overlap index. Pair wise comparisons were made between different years (with yearly samples clustered together) and between different samples individually. Sample size prevented investigation of dietary differences associated with sex, maturity class and season. The ecology of main prey is used to infer the predators' foraging strategies in the region.

Sowerby's trophic level (TL) was estimated as follows:

$$TL = 1 + \sum_{i=1}^{G} DC_i TL_i$$

where DC_i represents the numerical frequency of prey (i), TL_i the trophic level of prey (i), and G the total number of prey. Trophic level of prey species was extracted from Cherel et al. (2009) and Froese and Pauly (2010). For items identified to genus, the regionally most abundant species were used based on the work of Sutton et al. (2008); for items identified to family, the trophic level from other species found in this study within the taxon were used.

3. Results

Information on the stranding events and specimens is summarized in Table 1. The mean number of prey items per stomach was 85 ± 89.1 (range: 12–238), with fish occurring in 100% of the stomachs and cephalopods in 30%. Fish numerical frequency was 99.3% ($N=885$) (Table 2) and cephalopods comprised less than one percent of the total number of prey items ($N=8$) (Table 2). Fish otoliths from 15 families and cephalopod lower beaks from three families were identified, representing 22 taxa in total. Fish otoliths ranged from 22 to 235 otoliths (corresponding to 12–214 fish) per whale stomach. Cephalopods reached a maximum numerical frequency of 6.5% in a single individual (Mbi 09IIB). The high degree of erosion of the mandibles in this case suggests a long period of time since ingestion.

Fish eye lenses were present in most of the samples from 2009, namely Mbi 09IB (15), Mbi 09IIA (200–300), Mbi 09IIB (3) and Mbi 09IIC (73). Two eroded fish vertebrae and one scale were collected from Mbi 09IB. Cephalopod eye lenses were present in Mbi 09IIA (1) and Mbi 09IIB (1). Only one out of the four cephalopod beaks was considered fresh (*Taonius pavo*, Mbi 09IIA; Piatkowsky and Putz, 1994). No other soft tissue remains were collected and there was no record of artificial elements such as plastic or any other debris. All samples are stored and available at the Department of Oceanography and Fisheries, University of the Azores.

Table 3 summarizes information on prey indexes and ecology, including frequency of occurrence for prey with high numerical frequency. Myctophids were the most represented family, always above 30% in number, reaching 100% in stomachs with few contents. These occurred in all stranded individuals, followed by families Diretmidae and Opisthoproctidae, while the remaining fish families were represented by scarce or single occurrences. Demersal (benthopelagic) species such as *Galeichtyes* sp.?, *Guttigadus latifrons*, *Gadiculus argenteus* or *Epigonus telescopus* were rare ($\leq 1\%N$; Table 2). Main prey maximum sizes are below 15 cm (Froese and Pauly, 2010), and average prey size found in this study should be lower (*D. argenteus* common size around 9 cm). One exception is *Galeichthys* sp. (probably *feliceps*), which is normally around 35 cm (Froese and Pauly, 2010).

Schoener (1968) overlap index indicated significant overlap in the diet of whales stranded in different years, with the lowest values occurring when we compare the years 2005 and 2009, possibly due to the small sample sizes (small number of contents in 2005). Individual stomach comparisons revealed significant overlap for all samples, except for the 2005 samples. Trophic level compensated for all prey items was estimated at 4.4 ± 0.46, a value common to most of the myctophid prey.

4. Discussion

All prey species and genera identified in this study are known to occur in the Azores (Santos et al., 1997), except the demersal *Merluccius* sp. and *Galeichthys* sp. The occurrence of *Merluccius* sp., probably *M. merluccius* (Linnaeus, 1758) in the region, is known from only one unpublished recent record. The species is distributed along the European coast down to Mauritania, with records extending to the Meteor seamount, south of the stranding area (Froese and Pauly, 2010). *Galeichthys* sp. is a more unexpected record. There are only four recognized species for this genus and only two occur in the Atlantic, more specifically on the coastal waters of SW Africa. So far, there are no valid records for this genus on the central or northeast Atlantic (Froese and Pauly, 2010). The record of Lampe (1914) of this species in the Azores waters was considered not valid by Santos et al. (1997), suggesting a possible "mislabelling of the specimens or jars".

It has been argued that stomach contents of stranded animals may not be truly representative of the feeding habits of healthy animals, revealing unusually high percentages of empty stomachs and differences in prey composition and relative abundance (Clarke, 1986; Selzer et al., 1986). None of the stomachs examined in this study were empty and our results indicate recent feeding activity in two cases. Most samples also come from mass stranding events, which reflect feeding habits more reliably than other strandings (Santos et al., 2007). Finally, the consistency of stomach contents over an 8-year period indicates this study reflects Sowerby's beaked whales' summer diet in the Azores and possibly a previous region of provenance.

The seasonal coincidence of the five stranding events, four of which are mass stranding events, gives little evidence on natural death. The pathological study of some of these strandings was still underway at the time of writing of this work and none of the possible agents could be ruled out (e.g. bio-toxins, seasonal diseases, acoustic traumas).

4.1. Diet composition

A restricted group of meso and bathypelagic fish formed the bulk of Sowerby's diet in the Azores from 2002 to 2009. The myctophids *Diaphus* sp., *Lampanyctus* sp., together with *Opisthoproctus soleatus*, *Diretmus argenteus* and *Melamphaidae* spp. (10 spp. are known in the Azores; Santos et al., 1997) are present in all years sampled (except for the small samples from 2005), representing 62% of all contents by number, with a frequency of occurrence averaging approximately 70% in all samples.

The relatively wide range of sizes among most of the prey species in this study (3–15 cm) makes it difficult to analyze the emphasis given by numerical frequencies to small prey in the diet (Table 3). In this sense, the numerical contribution of the two largest species should be noted, namely *D. argenteus* and

Table 2
Numerical frequency (%*N*) of the fish and cephalopod identified in the stomachs of Sowerby's beaked whales (*Mesoplodon bidens*) stranded in the Azores islands from 2002 to 2009; *N* indicates minimum number of individual prey estimated from otoliths and lower beaks; family taxa organized by decreasing %*N* and cephalopods grouped together.

Prey list of lower taxa	Mbi 02I 27.07.2002		Mbi 02II 29.07.2002		Mbi 04I 19.07.2004		Mbi 05IA 21.07.2005		Mbi 05IB 22.07.2005		Mbi 09IA 28.07.2009		Mbi 09IB 29.07.2009		Mbi 09IIA 30.07.2009		Mbi 09IIB 30.07.2009		Mbi 09IIC 31.07.2009		Totals	
	N	%*N*	*N*	%*N*	N	%N	*N*	%*N*	*N*	%*N*	*N*	%*N*	*N*	%*N*	*N*	%*N*	*N*	%*N*	*N*	%*N*1	*N*	%*N*
Myctophidae																						
Myctophidae spp.			27	15.25											18	8.41	2	6.25	1	1.18	48	5.38
Diaphus sp.	8	14.04	15	8.47	25	10.50	13	100.00	11	91.67	36	73.47	10	66.67	36	16.82	13	40.63	10	11.76	177	19.82
Electrona risso					3	1.26					3	6.12	3	20.00	12	5.61					21	2.35
Lampanyctus sp.	20	35.09	32	18.08	47	19.75					1	2.04							30	35.29	130	14.56
Bolinichthys sp.?											2	4.08	1	6.67	58	27.10					61	6.83
Diretmidae																						
Diretmus argenteus	3	5.26	14	7.91	21	8.82					3	6.12			3	1.40	1	3.13	1	1.18	46	5.15
Melamphaidae																						
Melamphaidae spp.	8	14.04	27	15.25	56	23.53									13	6.07	4	12.50	10	11.76	118	13.21
Poromitra capito											2	4.08									2	0.22
Melamphaes typhlops?											1	2.04									1	0.11
Opisthoproctidae																						
O. soleatus	1	1.75	15	8.47	8	3.36									44	20.56	6	18.75	14	16.47	88	9.85
Ariidae																						
Galeichthys sp.?			3	1.69	6	2.52															9	1.01
Microstomatidae																						
Nansenia sp. ?															2	0.93			6	7.06	8	0.90
Scopelarchidae																						
Scopelarchus sp.	3	5.26																			3	0.34
Gadidae																						
Gadiculus argenteus					1	0.42													1	1.18	2	0.22
Melanonidae																						
Melanonus zugmayeri					2	0.84															2	0.22
Epigonidae																						
Epigonus telescopus																			1	1.18	1	0.11
Gonostomatidae																						
Gonostoma denudatum																			1	1.18	1	0.11
Moridae																						
Guttigadus latifrons					1	0.42															1	0.11
Macrouridae																						
Odontomacrurus murrayi															1	0.47					1	0.11
Merlucciidae																						
Merluccius sp.					1	0.42															1	0.11
Paralepididae																						
Paralepis sp.					1	0.42															1	0.11
Cranchiidae																						
Taonius pavo															1	0.47					1	0.11
Cycloteuthidae																						
Discoteuthis laciniosa			1	0.56																	1	0.11
Histioteuthidae																						
H. meleagroteuthis															1	0.47	1	3.13			2	0.22
Unidentified cephs			1	0.56	2	0.84											2	6.25			5	0.56
Unidentified fish	14	24.56	43	24.29	64	26.89			1	8.33	1	2.04	1	6.67	25	11.68	3	9.38	10	11.76	162	18.84
Total	57	–	177	–	238	–	13	–	12	–	49	–	15	–	214	–	31	–	85	–	893	100

Galeichthys sp., which average 27 cm and 55 cm, respectively. Prey size or weight estimations based on mesopelagic fish otoliths were not possible, due to the lack of biometric regression equations. This information seems absent from current literature, and it is of major relevance as it assists further analysis of these results, such as for biomass estimates. Nevertheless, prey preference studies based on numerical occurrence is a useful approach when combined with *in situ* abundances as developed below (e.g. Hansson, 1998).

4.2. Feeding activity and prey ecology

The meso and bathypelagic fish communities just north of the stranding area were described during one of the stranding periods (27 June to 01 July 2004; 42.81–41.24°N; Sutton et al., 2008). A large vertical migrating mesopelagic fish assemblage occupies the upper 0–750 m, termed the "Lanternfish group". Characterized by high diversity and low abundance, compared with the more productive areas to the north of the Mid-Atlantic Ridge, it is dominated by the Myctophidae family (29 spp., 50.8%*N*, 26.9% in biomass; Sutton et al., 2008).

Myctophids represent 49% by number of the Sowerby's beaked whale diet in this study. The most important prey, *Diaphus* sp. and *Lampanyctus* sp., are amongst the most abundant species in the Azores region, ranking in the top 10 at these depths (Sutton et al., 2008). It seems relevant to note they account for 34% in our study while reaching only 5.6% in net surveys. This could indicate possible prey or habitat preference, once *Diaphus* spp. may be preferentially associated to bottom structures (F.M. Porteiro personal communication).

Between 750 and 1500 m there is a decrease in abundance and increase in biomass, with two discrete deep-meso/upper-bathypelagic assemblages, both co-dominated by *Cyclothone microdon*: one with three large melamphaid species and the second

Table 3
Most frequent prey items with indication of frequency in number (%*N*), frequency of occurrence (%*O*), number of possible species (spp.), Adult Max Lengths of all possible species in the region (AML, cm; *source*: www.fishbase.org) and vertical migration (M) and non-migration (NM).

Family	Lower taxon	*N*	%*N*	%*O*	2002	2004	2005	2009	spp.	AML	Migrate
Myctophidae	*Diaphus* sp.	177	19.8	100	x	x	x	x	7	6–15	M
Myctophidae	*Lampanyctus* sp.	130	14.6	50	x	x		x	2	8.5–13.8	M
Melamphaidae	*Melamphaidae* spp.	118	13.2	60	x	x		x	10	2.9–13.1	M and NM
Opistoproctidae	*O. soleatus*	88	9.9	60	x	x		x	1	10.5	NM
Myctophidae	*Bolinicthys* sp.?	61	6.8	30				x	4	4.5–15.3	M
Myctophidae	*Myctophidae* spp.	48	5.4	40				x	25	2.9–14.3	M
Diretmidae	*Diretmus argenteus*	46	5.2	70	x	x		x	1	27.6	NM
Myctophidae	*Electrona risso*	21	2.4	40		x		x	1	8.2	M
Ariidae	*Galeichthys* sp.?	9	1.0	20	x	x			1	55	NM
–	Cephalopods (all)	9	1.0	40	x	x		x	3[b]	–	M and NM
–	Fish spp. (< 1%*N*)[a]	24	2.7	–	x	x		x	–	–	–
–	Non identified fish	162	18.1	90	x	x	x	x	–	–	–
	Total	**893**	**100%**								

[a] Includes 12 different species.
[b] Three unidentified items not included.

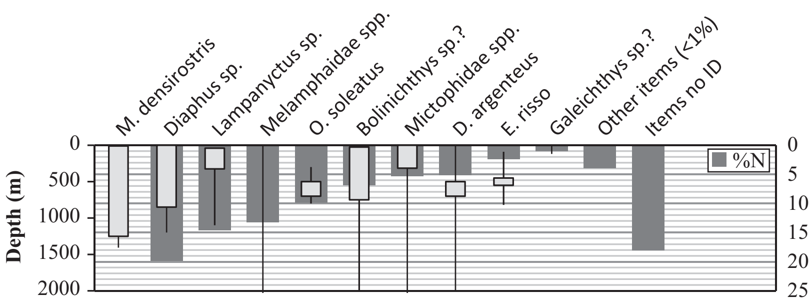

Fig. 2. Frequency in number (%*N*) of main prey, predator foraging depths (from *M. densirostris* off Canary Islands, Tyack et al., 2009; max depth given by Baird et al., 2008) and night-time distribution for vertical migrating prey: main depths for *O. soleatus* and *D. argenteus* (non migrators); Myctophidae (25 spp.) average values for night-time maximum depths are given; Melamphaidae (10 spp.) wide distribution depths not represented (source: Fishbase (Froese and Pauly, 2010)).

with the myctophid *Benthosema glaciale* (Sutton et al., 2008). Considering the numerical importance of the Melamphaidae species in our study, Sowerby's beaked whale foraging depths likely extends beyond 750 m, where this group of species becomes more abundant, though these could be also benefiting from night-time vertical ascension not contemplated on Sutton et al. (2008). According to Sutton et al. (2008) *D. argenteus* and one melamphaid (*S. mizolepis*) have important biomass contributions both in the upper and lower community, whereas the absence of *C. microdon* in any of our samples may indicate prey selectivity.

Main prey in the mid-Atlantic Azores region migrate to shallower depths at night aggregating in horizontal layers, becoming shallower than the maximum foraging depths (Baird et al., 2008; Tyack et al., 2009; Fig. 2). Diel patterns of vertical movements have been reported for several odontocetes, reflecting shifts in prey vertical availability (Benoit-Bird and Au, 2003) or predator avoidance (Baird et al., 2008). Recent studies on *Mesoplodon densirostris* off Hawaii revealed similar diving rates during day and night, leading Baird et al. (2008) to postulate that either prey do not exhibit diel vertical migrations, or that the whales switch prey species at night. Considering the importance of mesopelagic prey for *M. bidens* in this study, shallower foraging depths should occur during night-time.

4.3. Sowerby's beaked whale diet

Sowerby's beaked whales in the Azores are primarily fish eaters, as in other regions of its range (MacLeod et al., 2003; Spitz et al., 2011). Diet in the Azores contrasts to the mostly benthopelagic prey records from the few studies conducted elsewhere. Dix et al. (1986) reported a single Gadidae spp. from a stranded male in Newfoundland, on one of the first western Atlantic records. From Scotland, Santos et al. (1994, 1995) (see also MacLeod et al., 2003) reported 3 specimens, totaling 17 items, with *Merluccidae* spp. (52.9%) and *Gadidae* spp. (41.3%) being the most frequent prey. Gannon et al. (1998) reported on six freshly killed Sowerby's in the NE Atlantic, but 4106 food items were referred only asbottom-dwelling deep-water fish (deeper than 400 m) between 10 and 20 cm length. From the Bay of Biscay Siptz et al. (2011) reported three Sowerby's containing four Gadidae species (51.6%*N*), one *M. merluccius* and one Myctophidae, together with *Sepia* sp. and several swimming crab *Polybius* spp. (33%*M*).

According to these reports, Sowerby's near continental areas forage for neritic benthopelagic prey, probably in the lower shelf and shelf-break where these prey commonly occur (e.g., Mahon and Smith, 1989; Cartes et al., 2009). In the Azores, Sowerby's are feeding mostly on mid-water numerically abundant prey. Their advection through lateral currents and vertical entrapment over seamounts and island slopes are a long considered phenomena (Isaacs and Schwartzlose, 1965; Koslow, 1997), and foraging does occur near the bottom were these prey might also became available (Porteiro and Sutton, 2007). Many bottom dwelling fish reported as prey in other areas, such as *Merluccidae* spp. (Gannon et al., 1998) and *Gadidae* spp. (e.g. Spitz et al., 2011), achieve larger sizes than the main prey here reported, except for some of the scarce demersal and benthopelagics from this study. Sowerby's depredation on longline fishing gear has been recently suggested (Spitz et al., 2011), and although an artisanal bottom longline fishery extracts about 6000 tons per year of demersal fish species in this area (INE, 2009), mostly between 200 and 600 m depth (Morato et al., 2001), no prey with commercial value was found in our study, and there are no records of interactions of these whales with the Azorean bottom fisheries. The geomorphology of this insular and mid-Atlantic region and/or the actual scarcity of gadids and merluccids should provide explanatory variables for the regional differences in the feeding ecology. The regional prevalence of mid-water prey reveals dietary plasticity, which has been proposed by MacLeod et al. (2003) for all beaked whales, and is here revealed for Sowerby's beaked whales for the first time. Population level responses are expected when predators become subject to geographic variations in prey resources (e.g. Rutz and Bijlsma, 2006), and this should be taken into consideration in future population assessments.

There is as few data on Sowerby's diet as in its trophic level (TL). Early estimates by Ostrom et al. (1993) pointed to a TL of 3.7 based on stable isotope ratios (data corrected considering herbivores TL=2 following Pauly and Christensen, 1995). Pauly et al. (1998) calculated a 4.3 level for *M. bidens*, weighting grouped prey items from scarce existing records. Even though cephalopods were estimated to contribute 50%, which is not supported by any record to our knowledge, their values were very close to our estimate. The trophic level of 4.4 in this study reflects the predominance of myctophids and melamphaids and higher values are expected for other regions where larger species are being taken.

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